

A NEW LUNGFISH FROM THE LOWER CARBONIFEROUS OF VICTORIA, AUSTRALIA

By J. A. LONG AND K. S. W. CAMPBELL

Department of Geology, Australian National University, P.O. Box 4, Canberra, A.C.T. 2601.

ABSTRACT: *Delatitia* gen. nov. (type species *Ctenodus breviceps* Woodward), is described from a skull roof and isolated toothplates from the Lower Carboniferous Mansfield Group, Victoria. The new genus is similar to *Ctenodus* in the arrangement of bones B, C, D, I, J and L, but differs in having long E bones, a narrow Y1, Z not completely enclosed laterally by Y2, and the occipital sensory-line running posteromesially out of the I bones. Its toothplates have flat radiating tooth rows with the labial cusps conical and distally directed. The Y1 bones have a deep embayment for an opercular process.

Few Carboniferous fishes are known from Australia, most of the described taxa being from the Lower Carboniferous fluvial deposits of the Mansfield Group, eastern Victoria (Woodward 1906, Long 1982). The bulk of this material was collected late last century. It was studied initially by McCoy (1890) and later by Woodward (1902, 1906). Woodward assigned almost all of the species to genera known at that time from Europe, especially Scotland, but recent revision of the fauna shows that most of the species represent new genera (Long 1984, unpub. PhD thesis). In addition to the lungfish described in this paper the fauna comprises at least three genera of palaeoniscoids; a large rhizodontiform, *Strepsodus decipiens* Woodward (= *Pycnoctenion decipiens* Vorobjeva and Obrucheva 1977); and, three acanthodians, the commonest being *Gyracanthides murrayi*.

Fish faunas are known from two levels in the Mansfield Group. From the lower level the placoderms *Bothriolepis* spp., *Groenlandaspis* and a phyllolepid genus have been recovered (Long 1983), and hence it is clearly of Late Devonian age. Placoderms are absent from the upper level suggesting that it is post-Devonian in age, a view supported by the occurrence of the fish fauna mentioned above and lycopods of Carboniferous type (Marsden, 1976).

Ctenodus breviceps Woodward (1906) is the only Carboniferous lungfish known from the Southern Hemisphere. It is represented by a single skull roof and a few isolated remains, including toothplates and a partial tail. Although Woodward's sketch of the skull roof is accurate as far as it goes (Woodward 1906, fig. 3), preparation has clarified details of the bone pattern and revealed new data on the course of the laterosensory canals. These features preclude its assignment to *Ctenodus*.

The material is housed in the Museum of Victoria (NMV). Preparation of the holotype by vibrotool and chisel removed some of the matrix obscuring the skull roof bones. At least half the specimen is known only from the impression of the dorsal surface of the skull roof on the rock where weathering has removed the bone. This region of the holotype and the impressions of toothplates were studied from latex casts.

SYSTEMATIC PALAEOONTOLOGY

Class OSTEICHTHYES

Subclass DIPNOI

Genus *Delatitia* gen. nov.

ETYMOLOGY: From the Delatite River which runs through the Mansfield Basin.

TYPE SPECIES: *Delatitia breviceps* (Woodward) 1906.

DIAGNOSIS: Skull roof with a strongly concave posterior margin; B bone strongly waisted posteriorly and equal in length to the paired C bones anterior to it; D small, about three-quarters as long as B; Y1 narrow, L-shaped; Y2 partly but not completely embracing Z laterally; E bones elongate relative to C; I bones with prominent subdermal posterior processes. Occipital sensory line runs posteromesially out of the I-bones. Opercular with strongly developed anterodorsal process. Toothplates flat with more than eight radiating rows of co-linear cusps; outermost cusps form prostrate cones pointed distally. No cosmine on dermal bones.

REMARKS: The above diagnosis distinguishes *Delatitia* from *Ctenodus* by the course of the occipital sensory canal, shape of the Y1 and position of the Z. The toothplates are flat unlike the strongly arched multi-ridged toothplates of *Ctenodus*. The only other dipnoans which have a similar skull roof pattern, with a large B, paired C and small D, but without an isolated bone occupying the K position, are *Tranodis*, *Uronemus*, *Rhinodipterus* and an undescribed new genus from the Late Devonian Mt. Howitt site, Victoria. *Uronemus* is easily distinguished by the absence of toothplates, and any similarity between the roofing bone patterns is considered to be the result of convergence. *Tranodis* is a ctenodid with the Y series reduced and X correspondingly enlarged, an elongated B, and a squat E (Thomson 1965). All these features, together with the position of the occipital commissure, separate it from *Delatitia*. The undescribed new genus from Mt. Howitt differs from all of the above group by having I bones in mesial contact posterior to B. The remaining comparison is with the Late Devonian genus *Rhinodipterus* (as represented by *R. ulrichi*, Ørvig 1961). That species has overall similar proportions of roofing bones, and

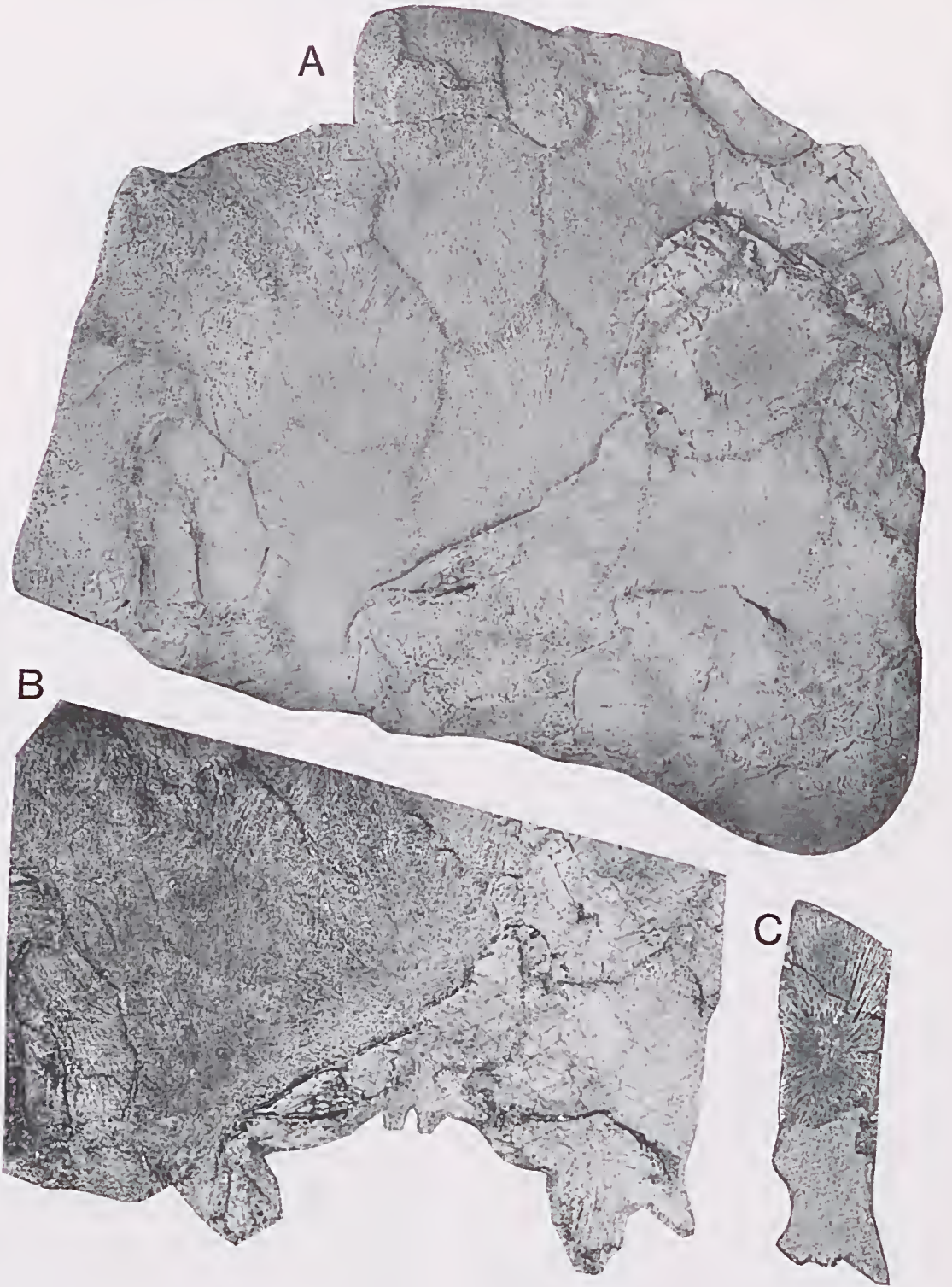


Fig. 1—*Delatitia breviceps* (Woodward) gen. nov. A, B, skull roof of holotype, NMV P10273; A, whitened with ammonium chloride; B, under alcohol. C, isolated E bone, NMV P179625. All natural size.

some individuals have a well-developed D bone. However, it has an ossified snout, cosmine-covered skull, and greatly reduced Y series.

In summary, *Delatitia* is not likely to be confused with any genus with which we are acquainted.

Delatitia breviceps (Woodward)

Figs 1-4, 5E

- 1906 *Ctenodus breviceps* Woodward, p. 15
 1958 '*Ctenodus breviceps*: Hills, p. 91.
 1965 *Ctenodus breviceps*: Gill, p. 17.
 1966 En Australie . . . *Ctenodus*: Lehman, p. 289.
 1967 *Ctenodus breviceps*: Andrews *et al.*, p. 644.
 1976 *Ctenodus breviceps*: Marsden, p. 22.
 1982 A dipnoan (Carboniferous) Long, p. 67.
 1982 ? *Ctenodus*: Long & Kemp, p. 704.
 1984 *Ctenodus breviceps*: Long & Turner, p. 241.

DIAGNOSIS: As for the genus.

MATERIAL: Holotype: NMV P20173, an almost complete skull roof. Other specimens: NMV P10257-P10259, natural moulds of toothplates. NMP 179625, an isolated E bone.

OCCURRENCE: From the upper section of the Mansfield Group near the intersection of Bridge Creek and Broken River, Mansfield, Victoria. Lower Carboniferous.

DESCRIPTION: *Skull roof.* Most of the skull roof, apart from the snout, is known from the impression of the dorsal surface on the rock. The left posterolateral corner has the vertical surface of the bone preserved. Overall the skull roof is gently arched with a shallow depression between the centres of the C and B bones. Numerous closely-spaced, narrow ridges emanate from the ossification centres of bones on the dorsal surface. No cosmine is present. The ratio of posterior breadth of the skull roof/length to the anterior of C is 1.38 for *Delatitia* compared to broader forms like *Ctenodus* in which this ratio is 1.8. The concave posterior margin of the skull roof features well developed subdermal processes on the I bones, with many small irregular processes bordering the whole margin. The lateral margins of Y1, Y2 and Z bones are straight except for a strongly developed notch in Y1 for an anterodorsal opercular process, similar to that found in *Sagenodus* (Watson & Gill 1923, fig. 20). The arrangement of the skull roofing bones is quite similar to that of *Ctenodus* (Fig. 5F) except for the position of the Z bone, which is only partially embraced laterally by the Y2 bone.

Bone B is completely preserved. It is pointed anteriorly and is strongly waisted posteriorly with a narrow posterior margin. The anterior half of B has an irregular suture with the C and J bones. No laterosensory canals or pit-lines pass through B or lie on its surface. Of interest is a pair of small foramina situated on the subdermal posterior fringe of B, possibly for the endolymphatic ducts. The I bones are complete on both sides. The dorsal surface is approximately as long as broad with a well marked anterior point where it meets J and Y1. The ventral surface of I, seen on the left side of the holotype, is marginally broader than long. The occipital sensory-line canal, exposed by preparation, runs

from the posterolateral corner through the centre of ossification to the posteromesial corner. The canal runs off I on the dorsal surface presumably onto the A bone. A short section of the middle pit-line (m.pl) is visible near the lateral margin of I. The C and J bones are completely preserved and are similar to those of *Ctenodus* in their shape, but are slightly narrower in proportion. The anterior margin of J has two concave margins for the X and L bones respectively. Bone X is partially preserved on both sides, being broader than long with a strongly convex posterior margin. Three short straight furrows, taken to be pit-lines, are present in the centre of X. The posteriormost L bone seems to be equidimensional with X, both of these bones being notably smaller than the I, J or C bones.

The Y1, Y2 and Z bones are clearly seen on the right side of the head in dorsal view. Y1 is unusually narrow, almost L-shaped with its longest axis being anterolateral. Y1 has a concave anterior margin, convex mesial margin and a strongly notched lateral margin which received a well developed anterodorsal opercular process. A small furrow, interpreted as a pit-line, is present on Y1. Y2 is almost equal in area to Y1 but is a straight, narrow bone, being almost as long as I or J but only half the breadth of these bones. A short sigmoid pit-line runs across the Y2-I boundary. Z is broader than long with convex anterior and mesial margins. The main lateral-line canal exits Z at the lateral section of the posterior margin and goes off the skull roof in a posterolateral direction.

D is nearly complete, missing only its anteriormost section. As there is inwards curvature of the lateral margins close to where the bone is cut off it is assumed to be almost complete. Bone D is ovate in outline as in *Ctenodus* but is slightly smaller relative to the size of B. Only the extreme posterior ends of the E bones are seen in the holotype, contacting the D, C and L bones. An isolated E bone (Fig. 1C) is long and narrow, having a breadth/length index of 28, quite unlike the E bones of *Ctenodus* species (*C. cristatus* E bones B/L=47, *C. interruptus* E bones B/L=39). The anteromesial corner of the E bone diverges slightly from the long axis of the bone, suggesting the presence of a small F. The centre of ossification of E is slightly anterior of centre.

A restoration of the head is given in Fig. 3. The proportions of the snout are conjectural, being based mainly on the length of the lingual ridge of the mandibular toothplate and the length of the isolated E bone.

TOOTHPLATES: Three imperfect toothplates from the Mansfield Group are presumed to belong to *Delatitia* as this is the only dipnoan known from the fauna. They are all preserved as natural moulds devoid of any bone or dentine. Woodward figured and described these specimens as anterior prepectoral spines of the acanthodian *Gyracanthides murrayi* (Woodward 1906, pl. 1, figs 3-6), but Hills (1958, p. 91) recognised them as dipnoan toothplates. Specimen NMV P10257, is the most complete individual, but it lacks the distal ends of most of the ridges and the heel of the plate, so that the overall form cannot be determined. The first ridge is dispropor-

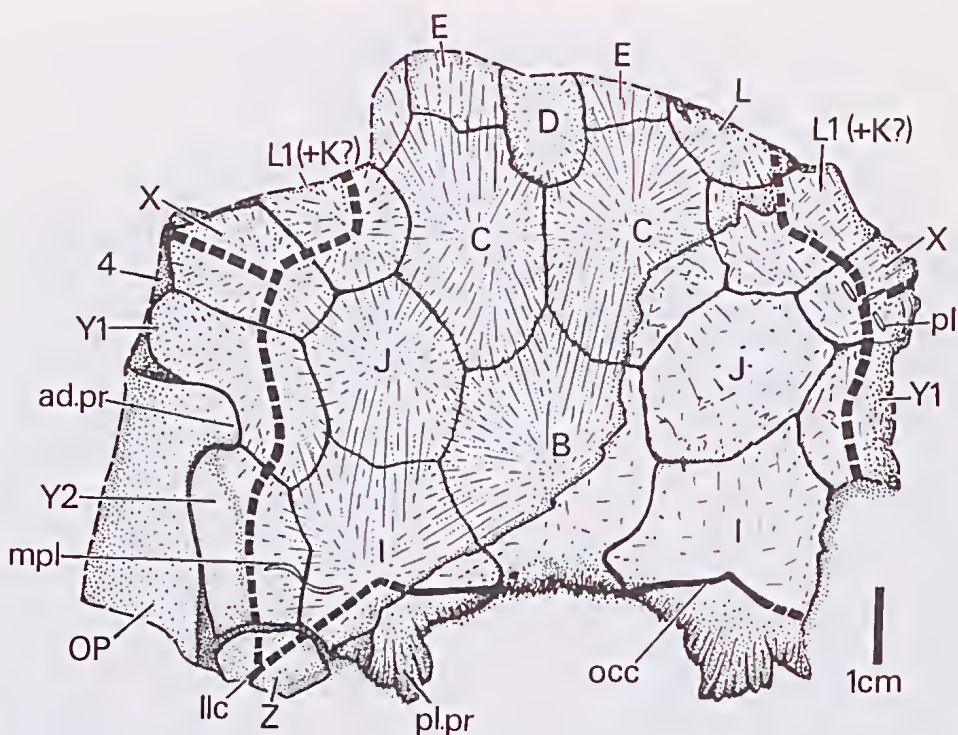


Fig. 2—*Delatitia breviceps* (Woodward) gen. nov. Skull roof of holotype, NMV P10273. Broken lines indicate presumed course of laterosensory-canals. Abbreviations: B, C, D, E, I, J, L1, L2, X, Y1, Y2, Z, 4—bones of the skull roof; ad. pr, anterodorsal process of opercular; llc, main lateral line canal; mpl, middle pit-line; occ, occipital sensory-line canal; OP, opercular; pl, pit-lines on the X bone; pl.pr, posterior subdermal process of the I bone.

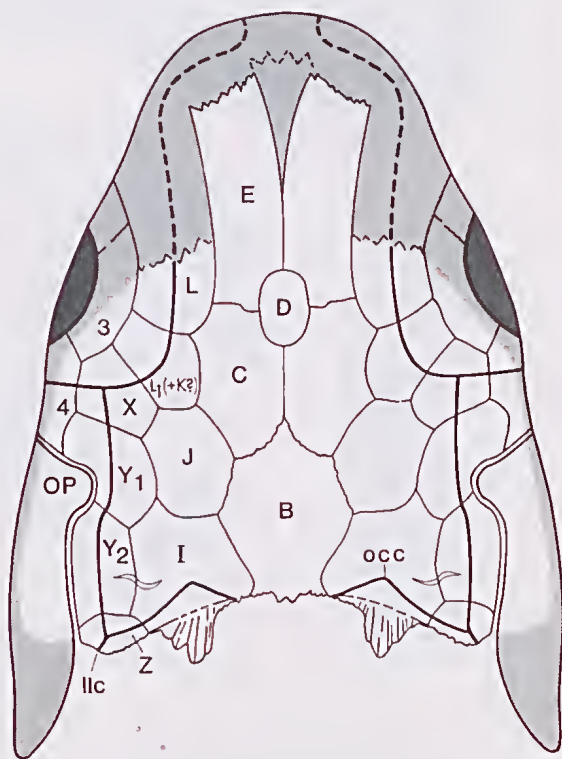


Fig. 3—*Delatitia breviceps* (Woodward) gen. nov. Attempted reconstruction of the head in dorsal view. Light stipple indicates areas which are not known from the material. The shape of bones 3 and 4 is based on the lateral margins of Y1 and X. Laterosensory canals shown as heavy black lines.

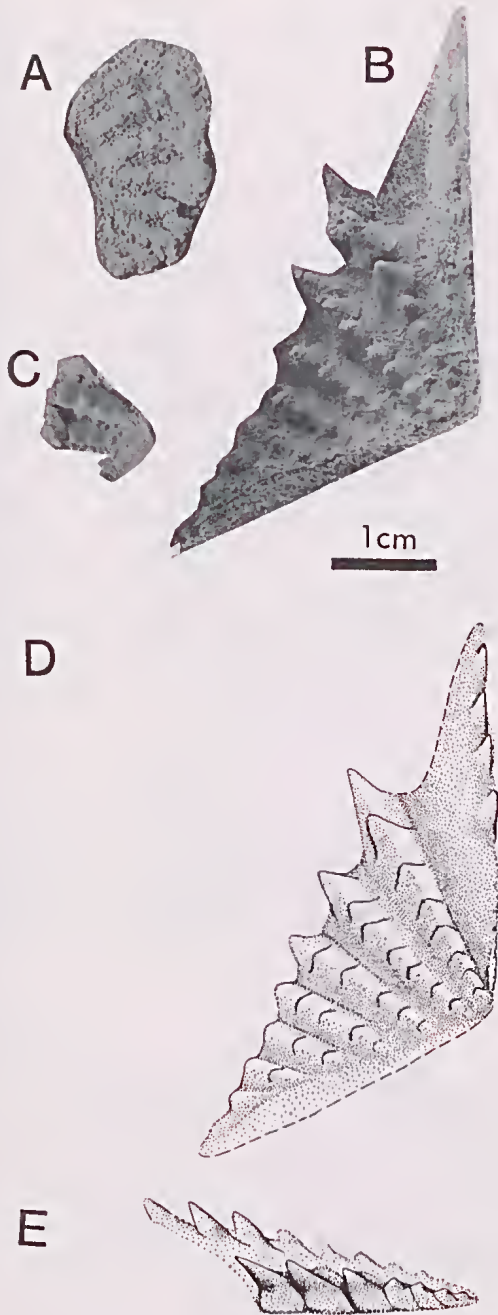


Fig. 4—*Delatitia breviceps* (Woodward) gen. nov. Toothplates. A, NMV P10258. B, NMV P10257. C, NMV P10259 (all $\times 2$). Latex casts whitened with ammonium chloride. D, attempted restoration of the left mandibular toothplate, based on NMV P10257. E, posterior oblique view of first two tooth ridges of NMV P10257. Partially restored outlines are shown by broken lines.

tionately longer than the posterior ridges and is separated from the second ridge by an unusually wide furrow (Fig. 4).

The mandibular toothplate of lungfishes can be distinguished by the longer first ridge which may curve mesially at its anterior extremity, and by being narrower in overall shape (e.g. *Rhinodipterus*, Gross 1956, Ørvig 1962; *Dipterus*, Jarvik 1967). NMV P10257 is identified as a left mandibular toothplate. It has a very long lingual ridge which has slight anteromesial curvature, and diverges from the second ridge at an angle of $ca\ 22^\circ$. There are at least eight teeth on each of the second and third ridges, diminishing to six and five on the fourth and fifth, but all the distal teeth may not be preserved. The first row has few anterior teeth preserved, these being long, conical to triangular prismatic in form, and directed anterolaterally. The teeth of the remaining rows have relatively flat sides meeting at a median crest so that all the teeth coalesce to form a co-linear ridge. The outermost teeth diverge from this ridge to point laterally and, in some instances, for example between the second and third cusps of the second row, there is a recess between the vertical sides of the individual cusp bases. Growth of each cusp over the preceding cusp can be barely seen by traces of growth lines. The other toothplates (NMV P10258, P10259) are incomplete and more worn than NMV P10257 but show the same type of array of cusps which have flat sides and coalesce into a median crest (Figs 4A, C).

DISCUSSION

In the overall roofing bone pattern, this new genus has obvious similarities to *Ctenodus*. The two genera have the same number of roofing bones disposed in approximately the same way, and they share a distinctive shape of the lateral bone canals from X to L. However, *Delatitia* retains two important primitive characters lost in *Ctenodus*—the larger Z which is not integrated into the skull roof, and the passage of the occipital commissure through a loosely attached bone A. *Conchopoma* is the only other post-Devonian genus with a similar bone Z and the occipital commissure in a loose bone A, but that genus has a denticulate palate and has lost its C bones (Sehultze 1975). The similarities with *Delatitia* are of no significance in interpreting relationship. In the shape of Z and the position of the occipital commissure, *Delatitia* is similar to several Late Devonian genera (Fig. 5A-D), among which *Rhinodipterus* of the *R. ulrichi* type has the most comparable roofing pattern. As Miles (1977, p. 241) has indicated, many specimens of that species retain a D bone. However, there are several major differences between *R. ulrichi* and *D. breviceps*—*R. ulrichi* has eosmine-covered bones, an ossified snout, and a single Y bone, the first two features being primitive and the third being advanced. The roofing bone pattern of *D. breviceps* also has several features in common with the Late Devonian *Scaumenacia curta*, particularly the squat B bone, the Y2 notched to receive the process on the anterodorsal corner of the opercular, and the unintegrated Z bone.

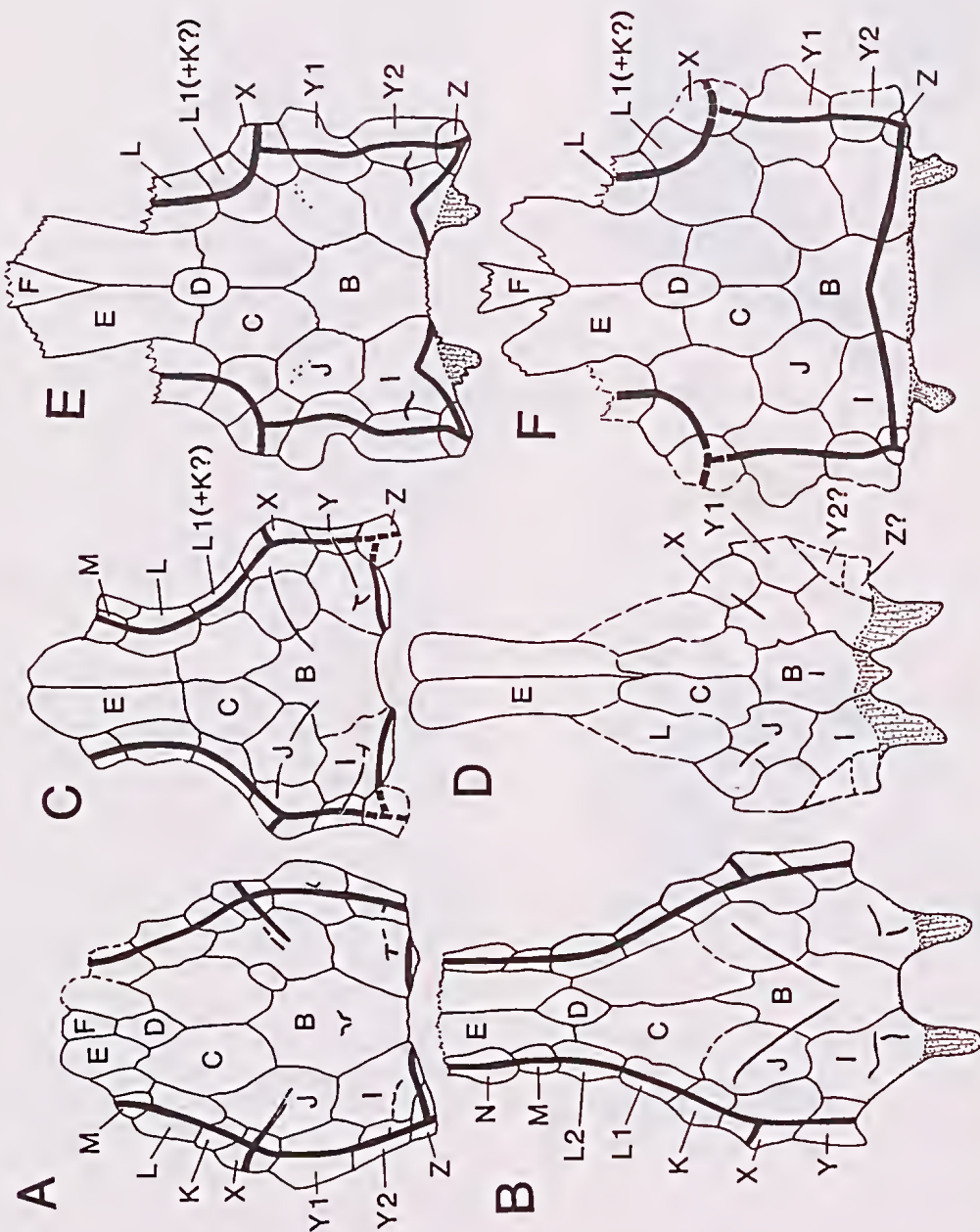


Fig. 5—Comparison of certain Palaeozoic dipnoan skull roof patterns. Laterosensory canals in heavy black lines, broken lines where uncertain. A, *Chirodipterus australis* (from Miles, 1977). B, *Rhinodipterus secans* (from Thomson and Campbell, 1971). C, *R. ulrichi* (from Ørvig, 1961). D, *Oerwigia nordica* (modified from Lehman, 1959). E, *Delatitia breviceps* (Woodward) gen. nov. F, *Ctenodus cristatus* (from Westoll, 1949). Not to scale.

Moreover, the cosmine has been lost. We note that despite the large number of specimens available, bones D and F have not been recorded in *S. curta*, and in these respects it is more advanced than *Delatitia*. *Sagenodus* also has a well developed notch in Y1, but the absence of C bones, the integated Z and the occipital commissure in B, all indicate that it has evolved independently, well beyond the stage reached by *Delatitia*.

The toothplates are of value in determining relationships. Important features are the elongate lingual ridge, the closely-packed teeth along the main parts of the ridges, and the recumbent conical distal teeth. These features are not characteristic of *R. ulrichi* or *S. curta*, though they are known in *Ctenodus* and in a number of isolated Late Devonian toothplates from Antarctica housed in the Australian Museum, Sydney (specimen numbers 54318, 54320, 54322, 54323). The lower toothplates of *Ctenodus* are strongly convex in profile whereas those of *Delatitia* are flat, but this difference is not of great significance. *Tranodis*, considered by some workers to be a ctenodid, apparently differs from both *Delatitia* and *Ctenodus* in the absence of Y2 and the shape of the whole X-L region. Such a placement for *Tranodis* seems improbable in view of the other features of the genus, especially the structure of the anterior part of the roof and the toothplates. The posterior part of the skull roof of *Tranodis* requires ruther study.

ACKNOWLEDGEMENTS

We thank Dr Tom Rich for the loan of material from collections in the Museum of Victoria. Mrs L. Wittig prepared Fig. 3, and Mrs M. MacDougall typed the manuscript. One of us (JAL) acknowledges receipt of a Rothmans Postdoctoral Fellowship.

REFERENCES

- ANDREWS, S. M., GARDINER, B. G., MILES, R. S. & PATTERSON, C., 1967. Pisces. In *The Fossil Record*, W. B. Harland, B. Gilbert-Smith and B. Wilcock, eds. Geological Society of London, London, 637-683.
- GILL, E. D., 1965. Fossils of Victoria. In *Victorian Year Book*, 79, Government Printer, Melbourne, 1-24.
- GROSS, W., 1956. Über Crossopterygier und Dipnoer aus dem baltischen Oberdevon im Zusammenhang einer Vergleichenden Untersuchung des Porenkanalsystems paläozoischer Agnathen und Fische. *Kung. svenska Vetensk Akad. Handl.* 4(5): 1-140.
- HILLS, E. S., 1958. A brief review of Australian fossil vertebrates. In *Studies on Fossil Vertebrates*, T. S. Westoll, ed., Athlone Press, London, 86-107.
- JARVIK, E., 1967. On the structure of the lower jaw in dipnoans: with a description of an Early Devonian dipnoan from Canada, *Melanognathus canadensis* gen. et sp. nov. *Zool. J. Linn. Soc.* 47: 155-183.
- LEHMAN, J. P., 1959. Les Dipneustes du Devonien du Groenland. *Medd. Groenland.* 160(4): 1-58.
- LEHMAN, J. P., 1966. Dipnoi et Crossopterygii. In *Traite de Paleontologie*, Vol. 4(3), J. Piveteau, ed., Masson, Paris, 243-412.
- LONG, J. A., 1982. The history of fishes on the Australian continent. In *The Fossil Vertebrate Record of Australasia*, P. V. Rich and E. Thompson, eds, Monash University, Melbourne, 53-85.
- LONG, J. A., 1983. New bothriolepid fishes from the Late Devonian of Victoria, Australia. *Palaeontology* 26, 295-320.
- LONG, J. A. & KEMP, N., 1982. Systematic and geographic index of Australian fossil vertebrates. Pisces. In *The Fossil Vertebrate Record of Australasia*, P. V. Rich and E. Thompson, eds, Monash University, Melbourne, 700-704.
- LONG, J. A. & TURNER, S., 1984. A checklist and bibliography of Australian fossil fishes. In *Vertebrate Zoogeography and Evolution in Australasia*, M. Archer and G. Clayton, eds, Hesperian Press, Perth, 335-354.
- MCCOY, F., 1890. Report on palaeontology for the year 1889. *Ann. Repts. Sec. Mines, Vict.* 1889: 23-24.
- MARSDEN, M. A. H., 1976. Upper Devonian-Carboniferous. In *Geology of Victoria*, J. G. Douglas and J. A. Ferguson, eds, Geological Society of Australia, Spec. Publ. 5: 77-124.
- MILES, R. S., 1977. Dipnoan (lungfish) skulls and the relationships of the group: A study based on new species from the Devonian of Australia. *Zool. J. Linn. Soc.* 61: 1-328.
- ØRVIG, T., 1961. New finds of acanthodians, arthrodires, crossopterygians, ganoids and dipnoans in the Upper Middle Devonian calcareous flags (Oberer Plattenkalk) of the Bergisch Gladbach-Paffrath Trough. *Palaeontol. Z.* 35: 10-27.
- THOMSON, K. S., 1965. On the relationships of certain Carboniferous Dipnoi with descriptions of four new forms. *Proc. R. Soc. Edinb. Sect. B. (Nat. Environ.)* 69: 221-245.
- THOMSON, K. S. & CAMPBELL, K. S. W., 1971. The structure and relationships of the primitive Devonian lungfish—*Dipnorhynchus susmilchii* (Etheridge). *Bull. Peabody Mus. Nat. Hist.* 38: 1-109.
- SCHULTZE, H.-P., 1975. Die Lungenfisch-Gattung *Conchopoma* (Pisces, Dipnoi). *Senckenb. Leth.* 56: 191-231.
- VOROBEVA, E. & OBRUCHIEVA, D., 1977. Rhizodont Crossopterygian fishes (Family Rhizodontidae) from the Middle Palaeozoic deposits of the Asiatic part of the U.S.S.R. In *Ocherki Po Filoginii e Systematik Iskopaemyekh Rvib i Beschelyustnyakh*, Nauka Moskva (in Russian), 89-97.
- WATSON, D. M. S. & GILL, E. L., 1923. The structure of certain Palaeozoic Dipnoi. *J. Linn. Soc. Lond.*, 25: 163-216.
- WESTOLL, T. S., 1949. On the evolution of the Dipnoi. In *Genetics, Palaeontology and Evolution*, G. L. Jepson, G. G. Simpson and E. Mayr, eds, Princeton Univ. Press, Princeton, 121-184.
- WOODWARD, A. S., 1902. Preliminary note on a Carboniferous fish fauna from Victoria, Australia. *Geol. Mag.* 9: 471-473.
- WOODWARD, A. S., 1906. On a Carboniferous fish fauna from the Mansfield District, Victoria. *Mem. natn. Mus. Vict.* 1: 1-32.